PATHOLOGICALLY DEFORMED *GRAPHOCERAS* (AMMONITINA) FROM THE JURASSIC OF SKYE, SCOTLAND

by NICOL MORTON

ABSTRACT. Successive populations of *Graphoceras* from the *concavum* Zone (Aalenian, Middle Jurassic) at Bearreraig (Isle of Skye, N.W. Scotland) contain an unusually high proportion (8·1%) of pathologically deformed specimens, in which the whorls grew over to one side after initial normal growth. Size-frequency distributions and proportions of dimorphs are similar among deformed and normal ammonites, and are consistent with random affliction of members of the populations. The most likely cause of the deformity is disease or parasitic infestation.

IN THE course of systematic and biostratigraphical work on the Aalenian and Bajocian ammonite faunas of the Bearreraig Sandstone in Skye and Raasay, western Scotland, successive populations of *Graphoceras* were collected from nodules in the *concavum* Zone (topmost Aalenian) in the lowest 9 m of the Udairn Shale Member (Morton 1965, 1976). The nodules formed at a very early stage of diagenesis, so that there is minimal post-burial crushing of fossils, and realization that the asymmetrical specimens described below were biologically deformed prompted careful examination to determine the frequency and types of deformity present.

PREVIOUS WORK

There is in the literature on Mesozoic ammonites a long history of observation, description and illustration of various types of deformity, reviewed and summarized by Spath (1945), Hölder (1956, 1970), Theobald (1958), Guex (1967), Bayer (1970), and Kennedy and Cobban (1976). Of relevance here, Buckman (1887–1907) discussed (Supplement p. 97) and figured (pl. 9, figs. 8–10) a specimen of *Graphoceras* from the Inferior Oolite of Bradford Abbas, Dorset, which shows irregular ribbing and umbilicus wider on one side but is otherwise symmetrical; also a *Fontannesia* from the same locality which shows deformity similar to that described below (pl. 47, figs. 8, 9). The only comprehensive studies of deformity in large samples of ammonites that I know of are by Guex (1967) and Bayer (1970).

Guex (1967) found 160 deformed specimens (2%) among some 8000 ammonites from the Toarcian of Aveyron, France, including 20 (2·5%) of 800 from the *bifrons* Zone. He found a wide variety of types of deformity all interpreted as resulting from injuries, and classified them according to the type of injury and the response of the animal into four groups: temporary (Group 1) or permanent (Group 2) disfigurement especially of ornament as a result of injury to the mantle only; imperfect replacement of a broken part of the shell (Group 3); and disruption of symmetry as a result of damage also to the 'centres of equilibrium' (Group 4). In the *Graphoceras* samples from Bearreraig the range of deformities is very much more limited, being confined to only Group 4 of Guex's study, in which the plane of symmetry of growth is affected. Incidentally, it can now be stated (cf. Guex 1967, p. 4) that this type of deformity can also occur in moderately involute as well as in evolute ammonites.

Bayer (1970) studied Aalenian and Bajocian ammonites from Swabia, southern Germany. Deformities related mainly to injuries were found to be most common (9·7%) in Stephanocerataceae (excluding Sphaeroceratidae), much less frequent in Sphaeroceratidae (1·4%) and Sonniniidae

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TABLE 1. Stratigraphical position and abundance of pathological ammonites, *concavum* Zone, Bearreraig, Isle of Skye.

Sample no.	Height above base of Udairn Shale Member	Total no. of ammonites recovered	Frequency of pathological ammonites	
			Number	Percentage
75/8	8·8 m	151	9	6·0
75/5	8·0 m	80	11	13·8
NES-B8	*c.* 6·0 m	5	1	(20·0)
75/4	5·4 m	69	4	5·8
75/3	5·0 m	68	5	7·4
NES-B5	3·0–4·5 m	24	2	8·3
Total	—	397	32	8·1

TABLE 2. Summary of details of deformed *Graphoceras* from the *concavum* Zone, Bearreraig, Isle of Skye.

Explanation of column heading abbreviations:

S. No.—Sample number (see Table 1 for stratigraphical details). M. No.—Allocated museum number, Hunterian Museum, University of Glasgow. Dim.—Dimorphic status (see Table 3): m—microconch with lappets; m?—probably microconch because of morphological similarity and closer final sutures; M or M?—probably juvenile macroconch because of morphological differences from microconchs of same size (see p. 3); ?—juveniles of uncertain dimorphic status [(m) more similar to microconch, (M) more similar to macroconch, but cannot be reliably assigned]. Max. D.—Maximum preserved diameter of specimen (A indicates aperture preserved). D. phr.—Diameter at end of phragmocone, beginning of body chamber. D. def.—Diameter at beginning of deformity. Wh. def.—whorl height at beginning of deformity. A. def.—Angular length (about axis of coiling) of deformed part, in brackets if incompletely preserved; T indicates deformity temporary. Dirn. def.—Direction of deformity, described as direction of displacement of keel from plane of symmetry, looking along venter towards aperture: R—displaced to right; L—displaced to left. Max. K-S.—Maximum distance of keel from projected plane of bilateral symmetry (defined from unaffected inner whorls). Beg. def.—Beginning of deformity: A—abrupt; G—gradual.

S. No.	M. No.	Dim.	Max. D.	D. phr.	D. def.	Wh. def.	A. def.	Dirn. def.	Max. K-S.	Beg. def.
NES-B8-4	S15319/2	?(m)	20·2	17·3	*c.* 10·5	4·2	(360)	L	1·5	A
NES-B5-6	S15322	m?	15·4	12·7	10·6	4·3	(190)	R	*c.* 2·1	A
NES-B5-7	S15325/1	m?	22·7	—	*c.* 11·7	*c.* 5·1	*c.* 390	R	2·8	?G
75/3-9	S26431/1	?	A20·8	15·6	*c.* 13·4	5·9	190	R	0·7	A
75/3-11	S26431/2	?(M)	16·0	15·1	12·4	5·5	34T	L	0·2	A
75/3-31	S26432	?	frag. of body chamber			15·5	?	R	?	G
75/3-54	S26433/1	?(m)	13·2	10·0	*c.* 8·5	?	*c.* 240	R	1·6	?
75/3-68	S26433/2	?	13·6	12·3	12·3	5·4	(60)	R	?	A
75/4-24	S26434/1	?(m)	15·3	12·2	*c.* 7·8	3·4	317	R–?L	1·0	G
75/4-44	S26434/2	m?	13·2	11·3	*c.* 5·9	*c.* 2·5	(410)	R–L–R–L	1·6	?G
75/4-55	S26434/3	?	11·0	8·4	9·9	4·3	(67)	R	1·2	A
75/4-57	S26434/4	?	21·8	?	< 14·8	?	(180)	L	0·6	?G
75/5-3	S26435/1	m	A25·0	*c.* 18·6	19·7	7·4	152	R	1·4	A
75/5-5	S26435/2	?(m)	21·7	15·2	?	?	(180)	R	2·1	?
75/5-17	S26436	M?	A34·4	*c.* 24·2	*c.* 14·0	?	*c.* 520	R	7·2	?G
75/5-20	S26437/1	M?	23·8	> 23·8	18·1	8·2	(165)	R	0·8	G
75/5-31	S26437/2	?	16·2	15·0	*c.* 10·7	4·4	60T	L	0·3	A
75/5-38	S26438	m	A34·2	24·0	*c.* 23·4	9·3	175	R–L	1·0	A
75/5-41	S26439/1	M?	30·2	*c.* 19·9	20·3	8·9	(193)	R	2·5	A
75/5-46	S26439/2	M?	25·2	*c.* 25·0	*c.* 8·7	*c.* 3·6	(526)	L–R	3·1	?
75/5-50	S26439/3	?	*c.* 22·4	17·2	*c.* 18·6	*c.* 8·7	(94)	R	1·1	G
75/5-56	S26440/1	m?	*c.* 21·6	19·7	*c.* 17·8	*c.* 7·8	(147)	L	1·4	G
75/5-64	S26440/2	?	12·9	11·3	10·4	4·6	(119)	R	0·5	A
75/8-22	S26441	M?	A *c.* 19·5	?	?	?	?	R	2·4	?
75/8-50	S26442/1	m?	15·9	*c.* 11·4	*c.* 11·4	?	(123)	R	0·9	A
75/8-57	S26442/2	m	A20·5	14·7	?	?	> 540	R	?	?
75/8-58	S26442/3	m?	16·0	15·3	*c.* 14·4	*c.* 5·4	(110)	R	1·3	?A
75/8-63	S26443	M?	27·1	*c.* 23·0	20·0	9·0	(166)	R	2·6	G
75/8-76	S26444	?(m)	23·1	?	21·1	8·9	(65)	L	1·0	G
75/8-81	S26445	M?	A *c.* 13·7	?	10·9	5·3	124	L	1·0	G
75/8-119	S26446/1	M?	*c.* 22·0	?	*c.* 15·0	7·4	(180)	L	0·7	?
75/8-124	S26446/2	?(m)	13·5	?	*c.* 9·2	3·8	(254)	L	0·7	A

(1·0%), and most rare in Graphoceratidae (0·3%). Variation in frequency of deformities was thought to be related to different modes of life.

OCCURRENCE

The stratigraphical levels of the *Graphoceras* samples (mainly from a shallow gully 300 m south of Bearreraig Point at grid reference NG 5186 5245) with total numbers of ammonites obtained and deformed specimens are given in Table 1. Details of the deformed ammonites are summarized in Table 2, including the Hunterian Museum (University of Glasgow) reference numbers. Measurements and other data on which Tables 2–4 and text-figs. 1–4 are based are deposited with the British Library, Boston Spa, Yorkshire LS23 7BQ as Supplementary Publication No. SUP 14019 (5 pages). These data may be purchased from the British Library; prepaid coupons for such purposes are held by many libraries throughout the world.

The frequency of occurrence of deformed ammonites in the samples from Skye is much higher than that found by Guex (1967) in the Toarcian of Aveyron, but is of the same order (9·7%) as that found by Bayer (1970) for Bajocian stephanoceratids in Swabia. The contrast between frequency of deformity in Swabian graphoceratids (0·3%) reported by Bayer compared with that for Skye *Graphoceras* is most striking. So also in comparison is the rarity of deformity in other Aalenian–Bajocian ammonite faunas from Skye. I know of no other published data with which to compare.

Detailed description and discussion of the fauna will be given elsewhere. There is a great range

TABLE 3. Dimorphic status (see text and Table 2 for explanation of categories) of deformed ammonites in each sample, with totals (and percentages) for each dimorphic category for deformed and normal ammonites; *concavum* Zone, Bearreraig, Isle of Skye.

Sample no.	m	m?	M?	?(m)	?(M)	?
75/8	1	2	4	2	—	—
75/5	2	1	4	1	—	3
75/4	—	1	—	1	—	2
75/3	—	—	—	1	1	3
NES-B8	—	—	—	1	—	—
NES-B5	—	2	—	—	—	—
deformed	3 (9·4%)	6(18·8%)	8(25·8%)	6(18·8%)	1 (3·1%)	8(25·0%)
Totals						
normal	59(16·2%)	28(7·7%)	82(22·5%)	18(4·9%)	14(3·8%)	163(44·8%)

TABLE 4. Direction of deformity of pathological ammonites; *concavum* Zone, Bearreraig, Isle of Skye (right–left convention used as looking along venter towards aperture).

Sample no.	Deformed to left	Deformed to right	Deformity direction varies
75/8	4	5	0
75/5	2	7	2
75/4	1	1	2
75/3	1	4	0
NES-B8	1	0	0
NES-B5	0	2	0
Totals	9	19	4

of variation within each population, but relatively little change between successive populations, so that for the present all are classified as variants of *Graphoceras* aff. *concavum* (Buckman). There is very marked dimorphism in the populations—microconchs with lappets (cf. *Graphoceras* (*Ludwigella*) *rudis* (Buckman)) are common, also apparently juvenile macroconchs of small to medium size, but large mature macroconchs (cf. *Graphoceras* (*Graphoceras*) *concavum* (Buckman) *sensu stricto*) are relatively rare. In general, microconchs tend to be more evolute and to have fewer ribs per whorl than macroconchs of comparable size, but there is much overlap in the ranges of variation so that many specimens cannot be identified with certainty as either dimorph. Of the 32 deformed specimens: 3 can be identified with certainty as microconchs because they show lappets (e.g. Pl. 56, figs. 5, 6); 6 are probably microconchs because of morphological similarity and supporting evidence of closer last two or three sutures (and in one specimen a constriction just behind the broken aperture; Pl. 56, figs. 17, 18); 8 are probably juvenile macroconchs because they are more involute and have closer ribbing and other morphological similarities (e.g. Pl. 56, figs. 1–4, 7, 8, etc.). The remaining 15 are dimorphically indeterminate juveniles, although 7 of these are more similar to one or other dimorph but without indicative morphological features. The numbers of specimens of each dimorphic category per sample are given in Table 3, with totals for each of deformed and normal specimens. The relative proportions of microconchs (m + m?) among deformed specimens is slightly higher than for the rest of the fauna (28·2 % cf. 23·9 %), but of macroconchs is of the same order (25·0 % cf. 22·5 %). It would appear, therefore, that the deformity has not been selective in which part of the populations was affected. Microconchs and macroconchs are deformed in almost equal proportions (9·4 % and 8·9 % respectively of each recognizable dimorph).

Comparison of the size-frequency distributions of deformed and normal ammonites (text-fig. 1), using diameter at the end of the phragmocone as the standard for comparison, shows no significant differences in range (except for the smaller and larger ends of the distribution) or mean diameter, though the latter is a statistic of doubtful significance in such a dimorphic set of populations. The modal classes are very nearly identical. Again it is evident that deformity does not selectively

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EXPLANATION OF PLATE 56

Pathologically deformed specimens of *Graphoceras* aff. *concavum* (Buckman), *concavum* Zone, Aalenian, Middle Jurassic, Bearreraig Sandstone Formation, Udairn Shale Member, 8·0 m above base (except fig. 9 from 5·0 m above base, and figs. 10, 11 from *c.* 6·0 m above base), south of Bearreraig Point, Trotternish, Isle of Skye.

Figs. 1–4. Juvenile macroconch, deformed to right so that umbilical diameter differs on opposite sides and with asymmetrical whorl cross-section; length of deformed part *c.* 520°; sample no. 75/5-17 (HMS 26436).

Figs. 5, 6. Microconch with lappets, deformed to right on last part of phragmocone and body chamber; sample no. 75/5-38 (HMS 26548).

Figs. 7, 8. Juvenile macroconch(?), deformed to right with gradual displacement of keel and venter; sample no. 75/5-20 (HMS 26437/1).

Fig. 9. Dimorph uncertain, temporarily deformed to left; sample no. 75/3-11 (HMS 26431/2) × 2·9.

Figs. 10, 11. Dimorph uncertain, deformed to left, whorl cross-section remaining approx. symmetrical; sample no. NES-B8-4 (HMS 15319/2).

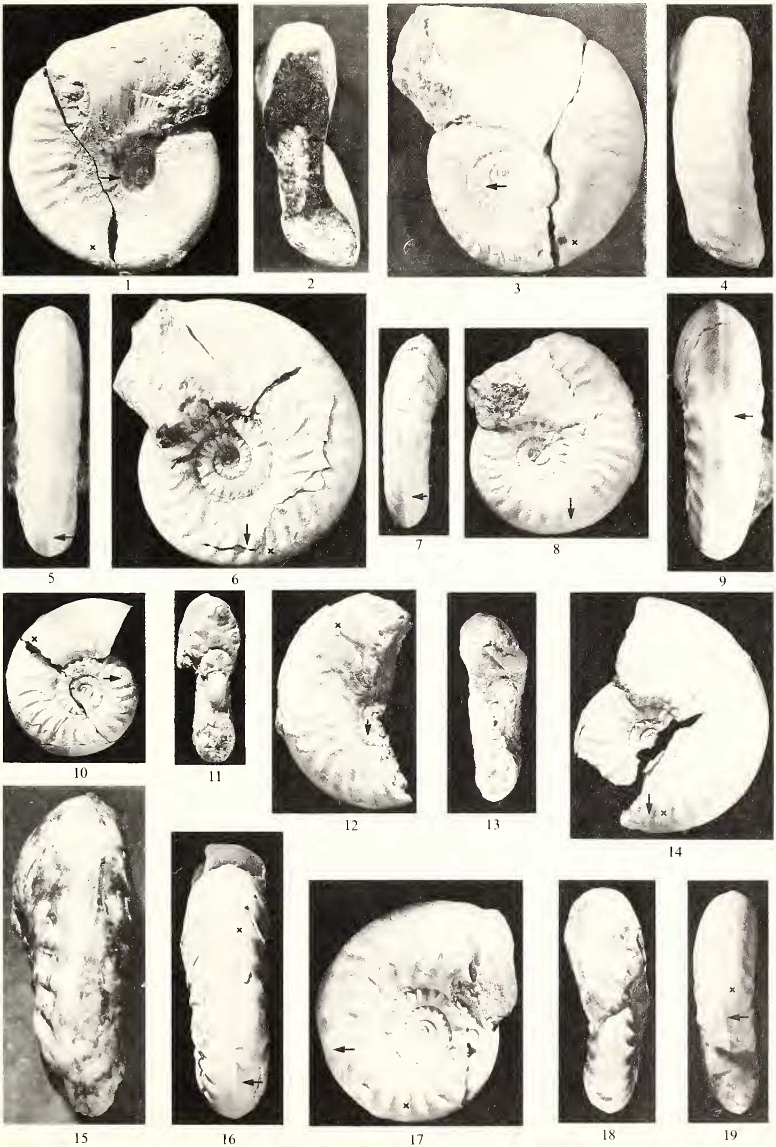
Figs. 12–13, 15. Juvenile macroconch(?), deformed to left on inner whorls (fig. 13) then to right on outer whorl with abrupt change in direction of keel and ventral lobe of suture 'anticipating' deformity; angular length of deformed part 526° of phragmocone plus body chamber; sample no. 75/5-46 (HMS 26439/2); fig. 15 only × 2·3.

Fig. 14, 19. Juvenile macroconch(?), deformed to right with abrupt change in direction of keel; sample no. 75/5-41 (HMS 26439/1).

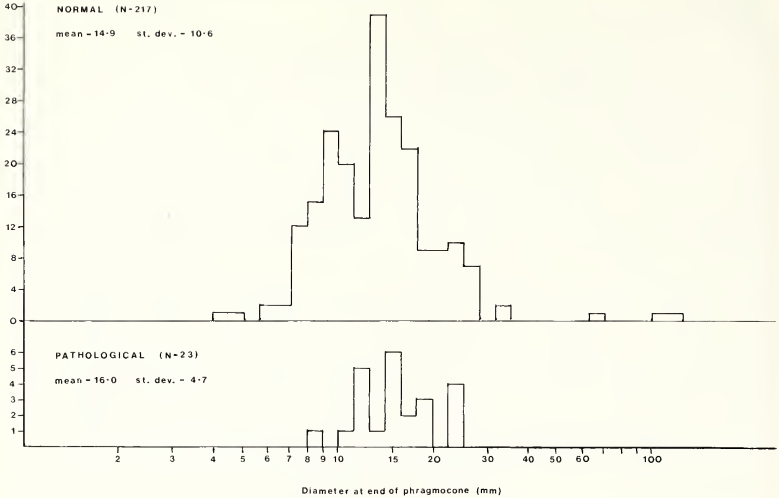
Fig. 16. Dimorph uncertain, deformed to right, but with gradual and abrupt slight changes in direction of keel; sample no. 75/5-64 (HMS 26440/2), × 3·8.

Figs. 17–18. Microconch with constriction behind aperture, deformed to right on body chamber with slight irregularity of coiling geometry of venter; sample no. 75/5-3 (HMS 26435/1).

All figs × 1·5 unless otherwise stated; specimens coated with ammonium chloride except figs. 2 and 15; + marks beginning of body chamber, and arrow indicates beginning of deformity.



MORTON, deformed *Graphoceras*



TEXT-FIG. 1. Size-frequency distribution of normal and pathological ammonites, *Graphoceras* aff. *concavum* (Buckman), *concavum* Zone, Bearreraig, Skye.

affect particular sizes within the populations. Nor, as is shown later, does it appear that the onset of deformity affected growth.

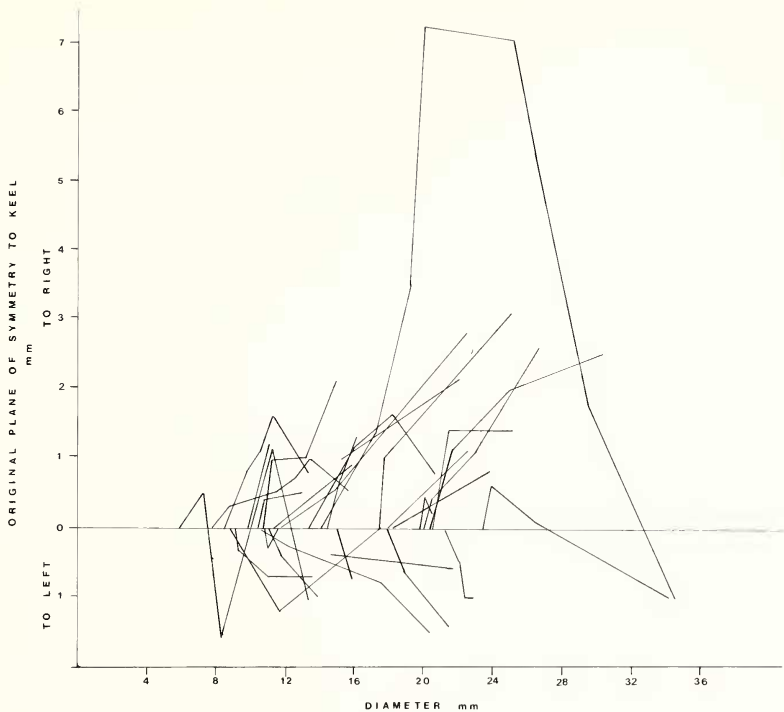
It has to be concluded from the above discussion that the deformity which affected the *Graphoceras* populations in Skye was non-selective in terms of dimorphism or size, and presumably also in age of individual. The distributions are consistent with random affliction.

DESCRIPTION OF DEFORMITY

The deformity found in the Skye *Graphoceras* populations is of only one type, affecting the bilateral symmetry of coiling of the specimens. Other types of deformity are extremely rare (one specimen shows evidence of slight injury affecting the ribbing temporarily) and are not discussed further.

Keel and Venter. Onset of deformity is particularly evident in departure of the keel (marking the mid-venter position) from the plane of bilateral symmetry as determined from the unaffected inner whorls. In most specimens where it can be estimated the maximum distance from the projected plane of symmetry to the position of the keel is less than 3 mm (see text-fig. 2), but in one (Pl. 56, figs. 1–4) it reaches a maximum of 7·2 mm at diameter 20·0 mm before decreasing.

The direction of displacement of the keel (looking along the venter towards the aperture) remains constant in most, with 19 displaced to the right (e.g. Pl. 56, figs. 14, 19), and 9 to the left (e.g. Pl. 56, figs. 10, 11) (see Table 4). The significance of this bias, which was found in all but one of the samples, is unknown. There remain 4 specimens in which the displaced keel and venter cross the original plane of symmetry from right to left or vice versa (e.g. Pl. 56, figs. 12, 13, 15). One (75/4–44) has the keel displaced to the right, then left, right and finally (at the last part preserved since the body chamber is incomplete) to the left. The right and left extremes of displacement are

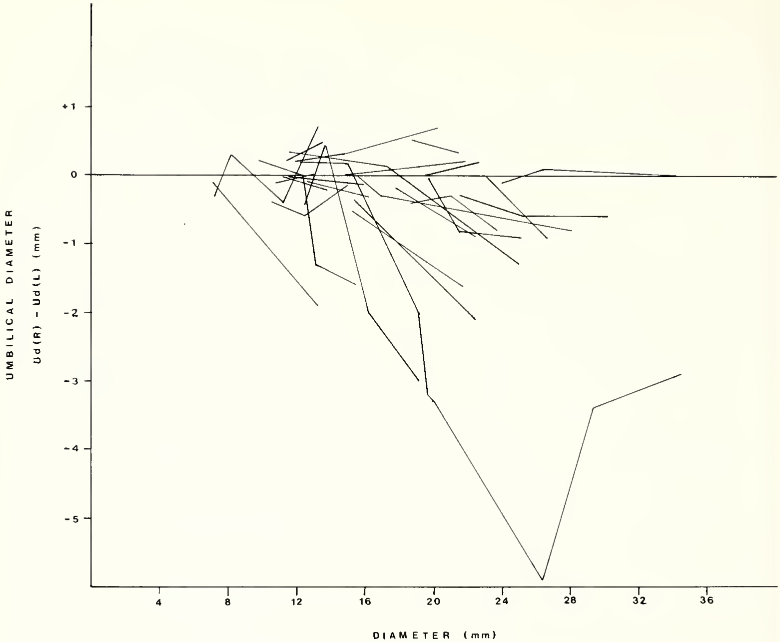


TEXT-FIG. 2. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye, measured as the deviation of the keel from the original plane of bilateral symmetry.

each one half whorl apart, but right and left 'axes' are not quite at right angles (70°). In none of the specimens has the deformity resulted in a new axis or plane of coiling being developed. In just over half (17, with 3 unknown) there is more than one change in direction of the keel, either increasing or decreasing the rate of departure from the original plane of bilateral symmetry.

The beginning of the deformity can be either abrupt, in the sense that there is an obvious change in the direction of the keel (e.g. Pl. 56, figs. 14, 19), or it can be so gradual that it can be difficult to see exactly where the keel first diverged from the original plane of symmetry (e.g. Pl. 56, figs. 7, 8). There are approximately equal numbers of the two categories (14 abrupt change, 12 gradual, and 6 indeterminate because of breakage, see Table 2). In some specimens both gradual and abrupt changes in direction of the keel are present (e.g. Pl. 56, fig. 16).

Once affected few recovered, and only two specimens show a return to the normal bilateral symmetry. In both the keel abruptly changes direction (both to left) followed by a more gradual change back to the original line, after angular distances of 34° (75/3–11, Pl. 56, fig. 9) and 60°

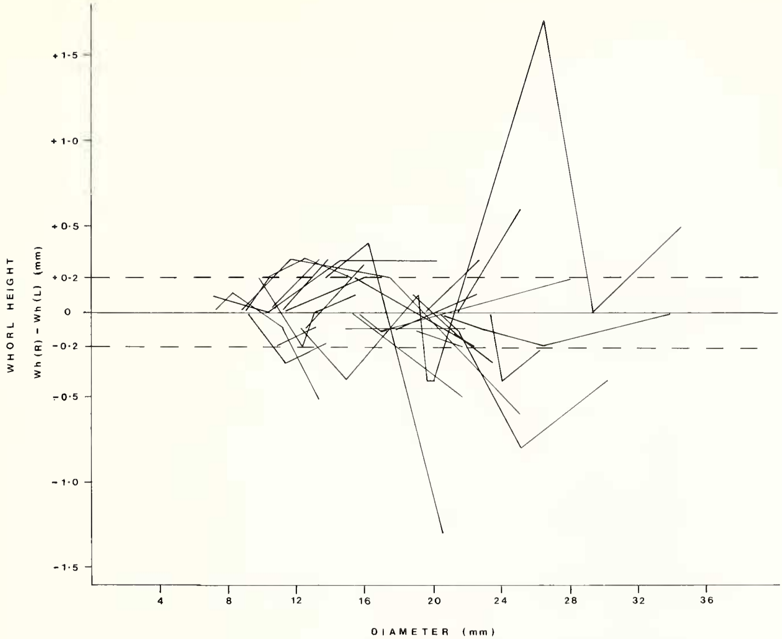


TEXT-FIG. 3. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye; loss of bilateral symmetry measured as the effect on umbilical diameter by subtracting Ud. on the left side from Ud. on the right side at the same position (Right/Left convention explained in text).

(75/5–31). Only 8 specimens have the deformed part completely preserved (i.e. including aperture) and in these the angular length of the affected part varies from 124° to about 520° (Pl. 56, figs. 1–4) or more. Another specimen (Pl. 56, figs. 12, 13, 15) shows 526° of phragmocone affected but lacks the body chamber. Clearly deformity did not cause cessation of growth—in the last case for at least a further two whorls. Only the body chamber is affected in 9 specimens (e.g. Pl. 56, figs. 17, 18); the last part of the phragmocone is also affected in 7 (e.g. Pl. 56, figs. 5, 6); but at least a quarter of a whorl of phragmocone is affected in 11 specimens (e.g. Pl. 56, figs. 10, 11).

Whorl shape and Umbilicus. In most specimens displacement of the keel and venter is followed by tilting of the whorl so that the umbilicus becomes narrower on one side than the other (text-fig. 3) (also compare Pl. 56, figs. 1 and 3). In some specimens the whorl shape remains basically symmetrical (e.g. Pl. 56, fig. 11) but with the plane of symmetry tilted to one side. In more extreme cases of deformity the upper part of the whorl is more pushed over, resulting in loss of symmetry with the whorl sides of differing height (text-fig. 4) and convexity (Pl. 56, fig. 2).

Shell geometry. Apart from aspects described above, the coiling geometry of the shell is little affected. Where there is a distinct or abrupt change in the direction of the keel, a notch in the



TEXT-FIG. 4. Deformity of *Graphoceras* from the *concavum* Zone, Bearreraig, Skye; loss of bilateral symmetry of whorl cross-section measured as the difference in whorl height on either side, by subtracting Wh. on the left side from Wh. on the right side at the same position (Right/Left convention explained in text). A difference of more than 0·2 mm results in visible asymmetry of the whorl cross-section.

spiral of the venter is just perceptible in side view (e.g. Pl. 56, fig. 17), sometimes with a very slight indentation. A few specimens also show a slight irregularity in the umbilical edge of the whorl.

Ribbing. Development of ribbing is not affected on deformed specimens more than is necessary to accommodate to varying whorl heights etc. on opposite sides (e.g. compare Pl. 56, figs. 1 and 3).

Sutures and Septa. Sutures and septa formed at the same time as the deformity began (i.e. half to three quarters of a whorl behind) are unaffected until the deformed part of the shell is reached. Then where visible the basic shape remains, even on the most severely deformed phragmocones, with only relative compression of the lobes and saddles on one side to accommodate to varying whorl heights. The centre of the external (ventral) lobe usually follows the divergence of the keel from the plane of symmetry, with a few exceptions. One (NES-B5-6) has the first three sutures after displacement of the keel remaining in the original plane of symmetry so that the keel is off centre of the external lobe, septal asymmetry being delayed. Conversely, another (75/5–46, Pl. 56, fig. 15) has two sutures before the deformity begins 'anticipating' the asymmetry so that the external lobes are further over to one side than the keel.

DISCUSSION

The deformities found in these *Graphoceras* from Skye are sufficiently similar to be interpreted as having the same cause. Occurrence has been shown to be random within the populations. Unexplained is the bias for displacement of keel and venter to the right rather than to the left—the ammonites are not thought to have had any asymmetry of organs which could have been differentially affected, nor is there any explanation in the suggested mode of life such as tendency to lie on one side.

Once affected, recovery was rare, with only two specimens showing a return to bilateral symmetry. However, continued growth was not influenced significantly, and sexual maturity (as microconchs) was attained by nine specimens. Therefore, although the effect on the animal's symmetry was dramatic, vital functions were not impaired.

The beginning of deformity is extremely gradual in some specimens and abrupt in others, but this is thought not to be significant because there are intermediate and varying conditions, and they are otherwise identical. In no case is there evidence of a distinct trauma, even after careful examination, and no evidence of shell repair, for example. Only the direction of shell growth is affected by the deformity, but not other aspects of shell morphology related to the growing edge (such as ribbing) or elsewhere (e.g. septal formation).

INTERPRETATION

Deformities of growth can result from three possible causes—genetic, injury, or infestation. Genetic defects must be regarded as highly unlikely, since all the deformed specimens have inner whorls which are normal, and only became affected by deformity in the outer whorls. I know of no genetic mechanism which will result in such abnormal growth after a relatively long period of normal growth.

Deformity as a result of injury is common among ammonites and well documented, with some groups more liable to be affected than others (Bayer 1970), and with a wide variety of types of deformity (e.g. Guex 1967; Hölder 1970). The effects of injuries on the shell are immediate and traumatic, involving a variety of repair mechanisms. Injury as a cause of the deformity in the Skye *Graphoceras* specimens described here seems unlikely for two main reasons. First, the deformities are all of one type, and it is more likely that injury, by whatever cause, would result in a greater variety of effects. Secondly, the beginning of deformity is as often as not gradual with no evidence of trauma, and this is not what would be expected as a result of an injury.

There remains the possibility that deformity was caused by part of the population being infested by parasites or infected by disease. This seems to me to be the most likely explanation because it would fit in with the random distribution through the population, with restriction of deformity to only one type, and with gradual or more abrupt beginning depending on the speed at which infestation took place. Attack by parasites was suggested by Keupp (1976, 1979) as the explanation for a variety of deformities among Jurassic ammonites from Franconia, southern Germany. None of these is comparable with that described here, either in type or in frequency of occurrence within a population. I know of no criteria to decide between infestation by disease or by parasites, but favour some form of infestation as being the most plausible explanation for the deformed *Graphoceras* in these populations from Skye. There is little evidence of similar deformity in modern *Nautilus* or coleoids, even among those affected by parasites. Living cephalopods offer little guidance to interpretation of the phenomenon described here.

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